GUIDELINES FOR PROTECTING SPOTTED TURTLES AND THEIR HABITATS IN MASSACHUSETTS

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INTRODUCTION

The Natural Heritage and Endangered Species Program of the Massachusetts Division of Fisheries and Wildlife (the Division) has developed the following guidelines to assist property owners, land managers, consultants, and conservation commissioners with protecting spotted turtles (*Clemmys guttata*) and their habitats. The spotted turtle is listed as a Species of Special Concern by the Division in Massachusetts, and activities proposed in or near its habitats are subject to review under Massachusetts laws. The Division intends to apply these guidelines in its review of Notices of Intent, pursuant to the Massachusetts Wetlands Protection Act regulations (310 CMR 10.59). Implementing these guidelines will also help property owners and land managers avoid potential violations of the Massachusetts Endangered Species Act (MGL c. 131A) and its implementing regulations (321 CMR 10.00).

Users of these guidelines are advised that they do not supersede any law, regulation, or official policy of this or any other agency. Rather, these guidelines are intended to complement existing regulatory review processes by providing scientifically based management recommendations. These guidelines include a summary of life history and habitat requirements of spotted turtles, a summary of pertinent laws and regulations, guidelines for avoiding adverse impacts to spotted turtles and their habitats, and literature cited.

LIFE HISTORY AND HABITAT REQUIREMENTS OF THE SPOTTED TURTLE

Spotted turtles inhabit a variety of wetland and upland habitat types (Table 1). Adults may be found in emergent marshes, shrub swamps, forested wetlands, seasonal pools, and forested and non-forested uplands. Spotted turtles are wary of people approaching and may be difficult to detect in wetlands, depending on the density of vegetation and clarity and depth of the water. When moving over land, adults are more conspicuous, but when they are resting on land and burrowed under leaf litter (for example, resting between daily movements) they can be easily overlooked. Hatchlings and juveniles are especially difficult to detect, and accordingly, we know very little about them.

Spotted turtles use both aquatic and terrestrial environments. During the active season (March through October), most adult spotted turtles in a population follow a similar pattern of activity: 1) emergence; 2) overland travel to a seasonal pool; 3) overland travel to a nest site and return to a seasonal pool (if female); 4) overland travel to an aquatic or terrestrial

estivation site; 5) overland travel to hibernacula (Joyal 1996, Milam 1997). Different configurations of wetlands and uplands (e.g. the absence of seasonal pools) may dictate activity patterns that vary from the one described above.

Adult spotted turtles spend up to 93 days of the active season on land – nesting, estivating, and traveling between wetlands (Milam 1997) (Table 1). They inhabit up to 3 different seasonal pools in one season (Joyal 1996). In September and October, adult spotted turtles return to their overwintering sites, which are usually in permanent wetlands. There they hibernate under hummocks and root masses (Joyal 1996, Milam 1997). Spotted turtles are also known to hibernate in flooded seasonal pools (Milam 1997).

Spotted turtles are capable of long-distance movements overland (Tables 2 and 3). The maximum straight-line distance that a spotted turtle has been known to move overland between wetlands is 1,150 m (Joyal 1996). The home range size of individual adult spotted turtles varies from 0.2 ha to 34.4 ha (Milam 1997). Average home range sizes range from 0.75 ha (Perillo 1999) to 3.7 ha (Haxton and Berrill 1999) (Table 2).

Mating has been observed during March, April, and May in Pennsylvania (Ernst 1976). Most nesting occurs in June, but can extend into early July (Ernst and Zug 1994). Clutch size ranges from 2 to 7 eggs per nest (Ernst and Zug 1994, Joyal 1996), and average clutch size ranges from 3.2 to 5.3 eggs per nest (Ernst and Zug 1994, Litzgus and Brooks 1998).

Spotted turtles travel 50 to 570 m overland to terrestrial nest sites (Milam 1997, Joyal 1996) (Table 3). Most spotted turtle nesting observations have occurred in open, non-forested habitat (Ernst 1970, Milam 1997, Litzgus and Brooks 1998). Nesting has also been observed on hummocks in emergent wetlands (Milam 1997).

Spotted turtle hatchlings emerge 70 to 125 days after egg deposition (Ernst 1970, Joyal 1996). Emergence occurs from late August through October (Ernst 1970, Joyal 1996). In Pennsylvania, some hatchlings were found to overwinter in their nests (Ernst 1976), but other researchers in the northern reaches of the spotted turtle's range have not documented this behavior (Joyal 1996).

Female spotted turtles reach sexual maturity when they are 75 to 85mm in plastron length, at which point they are estimated to be 8 years old (Ernst and Zug 1994). Males attain maturity when they are 78 to 82 mm in plastron length, when they are estimated to be 7 years old (Ernst and Zug 1994). Because these results came from a study in Pennsylvania, they may be underestimates of size of sexual maturity for turtles in Massachusetts (see Litzgus and Brooks 1998).

Adult spotted turtles are omnivorous, foraging in the water on such items as aquatic plants, algae, adult and larval insects, crustaceans, snails, tadpoles, salamander eggs and larvae, and carrion (Ernst 1976).

Table 1. General habitat types required by the spotted turtle.

Habitat type	Description	Habitat functions provided for spotted turtles	Time of year used by spotted turtles (in Mass.)
Wetland habitat	All wetland types are used by a population (e.g. ponds, forested swamps, marshes, fens, shrub swamps, streams, rivers, seasonal pools). Adults overwinter in permanent wetlands (e.g. swamps, ponds, marshes, rivers) as well as seasonal pools.	Overwintering, mating, nesting feeding, shelter, estivating, basking	Year-round
Upland habitat	Various upland types within 1,150 m of the wetland's edge. Overland travel occurs in forested and non-forested uplands. Nesting usually occurs in non-forested habitats.	Nesting, migrating, shelter, estivating, basking	April through October, with heaviest use from May through September

Table 2. Summary of home range sizes recorded for radio-tracked spotted turtles.

	Home range size (ha)				
Location	**Minimum**	**Maximum**	**Average**	**No. of individuals (duration of study)**	**Source**
Massachusetts	0.2	34.4	3.5	26 (2 seasons)	Milam 1997[1]
Connecticut (females only)	Not reported	Not reported	0.75	3 (1 season)	Perillo 1998[2]
Connecticut (males only)	Not reported	Not reported	2.4	2 (1 season)	Perillo 1998[2]
Ontario	0.4	6.8	3.7	15 (2 season)	Haxton and Berrill 1999[3]
Ohio	0.0	13.19	1.79	22 (4 seasons)	Lewis and Faulhaber 1999[4]
Indiana	0.24	6.3	2.17	16 (3 seasons)	Barlow and Kingsbury 1999[5]

1 – 100% minimum convex polygon method
2 – 95% minimum convex polygon method
3 – minimum convex polygon method
4 – 95% adaptive kernel polygon
5 – unknown method

Table 3. Summary of overland movements recorded for radio-tracked spotted turtles moving to nest sites.

	Straight line distance (m)				
Location	**Minimum**	**Maximum**	**Average**	**No. of individuals (duration of study)**	**Source**
Maine	70	570	247	14 (2 seasons)	Joyal 1996
Massachusetts	50	312	249	10 (2 seasons)	Milam 1997

Threats to Spotted Turtles – The greatest threats to existing populations of spotted turtles are those that increase the mortality (or removal from the wild) of adults and juveniles (Crouse et al. 1987, Congdon et al. 1993, Congdon et al. 1994). While significant and repeated losses of eggs and hatchlings can also lead to population decline, only slight increases in adult and juvenile mortality can have the same effect (Doroff and Keith 1990, Brooks et al. 1991, Congdon et al. 1993). Turtles require high survival rates because they – and other long-lived organisms – have evolved to balance their low reproductive rate with a long life span (see Gibbs and Amato 2000). In other words, they may require several decades of breeding before they succeed in replacing themselves in their populations.

Spotted turtles that survive their hatchling and early juvenile years (the period when survival rates are naturally low) have traditionally been able to depend on relatively long life spans. By adult size, their shells are an effective defense against most natural predators. However, humans have added – and continue to add – sources of mortality that turtles are poorly equipped to avoid, including: cars and trucks, farm machinery and landscape equipment, and removal for pets (which is the demographic equivalent of mortality).

These sources of mortality also act as barriers to spotted turtle movement, as do obvious physical barriers such as fences, curbs, railroad tracks, and retaining walls. Roads, for example, fragment turtle habitat and make dispersal more difficult or impossible, depending on width, traffic volume, and construction features of the road. Fragmentation may lead to isolation of local populations, and isolation can increase a population's risk of extinction (Saccheri et al. 1998). An isolated population cannot receive dispersing individuals from other populations, a process that may be necessary to maintain genetic diversity and to sustain the population.

The loss of diverse and connected wetland complexes – those containing seasonal pools as well as permanent wetlands – threatens spotted turtles. Since spotted turtles often nest in and move through open upland habitats (Joyal 1996, Milam 1997, Haxton and Berrill 1999), they are also vulnerable to activities that typically occur there. Plowing or otherwise excavating upland habitats can destroy nests and kill turtles. Mowing can also kill spotted turtles of all ages. Removal of the forest canopy in the immediate vicinity of seasonal pools can degrade wetland habitat quality by negatively affecting amphibians (Raymond and Hardy 1991, deMaynadier and Hunter 1999). The eggs and larvae of amphibians that breed in seasonal pools are an important food source for spotted turtles.

Nest predators, such as skunks and raccoons, threaten spotted turtle populations, and raccoons prey on adult spotted turtles as well (Ernst 1976). Providing attractants to these predators – such as exposed garbage, pet food, shelter – in or near spotted turtle habitat can adversely affect their reproduction. Human presence can also easily disrupt nesting activity. Because a spotted turtle is likely to abandon her nest if disturbed before she has started to lay her eggs, human recreation in spotted turtle habitat can have a negative impact. Recreation (without education and/or area restrictions) also leaves spotted turtles more vulnerable to collection for pets.

MASSACHUSETTS LAWS THAT PROTECT SPOTTED TURTLES AND THEIR HABITATS

Massachusetts Wetlands Protection Act – The Massachusetts Wetlands Protection Act (WPA) (MGL c. 131 s. 40) protects a variety of wetland "Resource Areas" (and, in some cases, the surrounding uplands) that can support rare, state-listed wildlife. According to the WPA's implementing regulations (310 CMR 10.00), projects that are proposed to occur in a Resource Area or associated 100-foot buffer zone, and that will alter wetland habitat of spotted turtles or other rare wildlife, may have "no short or long term adverse effects" on that habitat. Specific protected Resource Areas that spotted turtles are likely to inhabit include: Land Under Water Body; Isolated Land Subject to Flooding; Bordering Land Subject to Flooding; Bordering Vegetated Wetlands; and Riverfront Areas (Table 4). These are defined in detail in the WPA regulations.

The Division has prepared an atlas of "Estimated Habitats of Rare Wildlife," including estimated habitat of spotted turtles. The atlas is available from the Division and from local conservation commissions. When a proposed project will occur within an Estimated Habitat, a copy of the project proponent's Notice of Intent to the local conservation commission must be forwarded to the Division. Within 30 days of receipt of the Notice of Intent, Division staff determine: 1) whether the proposed project would occur within actual habitat of a rare species; and, if so, 2) whether the proposed project will have any "short or long term adverse effects" on that wetland habitat. The Division submits their opinion to the applicant, the local conservation commission, and the Department of Environmental Protection. The Division's opinion is presumed correct, although it may be rebutted by clear evidence to the contrary.

The important wildlife habitat functions protected under the WPA are: feeding, breeding, migrating, overwintering, and finding shelter. Therefore, adverse impacts to habitats supporting these activities are not permitted. Replicating habitat for wetlands wildlife and moving animals to new habitat are not permitted because adverse impacts to existing habitat still occur. According to the Department of Environmental Protection's rare species policy, "habitat replication, relocation of individual animals, or other proposed measures purported to offset adverse effects shall not be permitted because these activities cannot meet the performance standard of no adverse short or long term effect on the habitat of the local population" (DEP Rare Species Policy 90-2).

Table 4. Resource Areas (pursuant to Massachusetts Wetlands Protection Act) and associated habitat functions provided for spotted turtles.

Resource Area[1]	**Feeding**	**Breeding** (mating & nesting)	**Migrating**	**Overwint-ering**	**Shelter**	**Comments**
Land Under Water Body	adults juveniles hatchlings	adults	adults juveniles hatchlings	adults juveniles hatchlings	adults juveniles hatchlings	A pond and its buffer zone can provide habitat for most life stages.
Isolated Land Subject to Flooding (ILSF)	adults juveniles hatchlings	adults	adults juveniles hatchlings	adults juveniles hatchlings	adults juveniles hatchlings	ILSF may contain seasonal pools and other shallow wetlands used by turtles of all ages.
Bordering Land Subject to Flooding (BLSF)	adults juveniles hatchlings		adults juveniles hatchlings		adults juveniles hatchlings eggs	BLSF may contain seasonal pools and other shallow wetlands used by turtles of all ages.
Bordering Vegetated Wetlands (BVW)	adults juveniles hatchlings	adults	adults juveniles hatchlings	adults juveniles hatchlings	adults juveniles hatchlings eggs	BVW may provide wetland habitat for turtles of all ages, and its buffer zone may support nests.
Riverfront Area	adults juveniles hatchlings	adults eggs hatchlings	adults juveniles hatchlings	adults juveniles hatchlings	adults juveniles hatchlings eggs	A Riverfront Area can provide various wetland habitats, and its adjacent uplands can provide all habitat functions mentioned here.

1 All Resource Areas (except Isolated and Bordering Land Subject to Flooding) include a 100-foot buffer zone in which activities can be regulated if they will adversely affect the Resource Area itself. Riverfront Areas consist of adjacent uplands up to 200 feet from the high water line of a river or perennial stream. The uplands within the Riverfront Area are regulated as part of the Resource Area.

Assessing Impacts Under the WPA – To expedite regulatory reviews of large projects, projects with direct wetland alterations, and projects with significant buffer zone loss, applicants should follow the guidelines below.

- Applicants are strongly encouraged to conduct rare wildlife habitat evaluations prior to filing a Notice of Intent. Such evaluations are more likely to expedite the review process if conducted by a wildlife biologist with proven experience and expertise conducting surveys for the target species, in this case, the spotted turtle. The applicant should use the information provided in the evaluation to determine whether his or her project would adversely affect rare species habitat.

- Submit the full Notice of Intent to the Division, including plans, stormwater management forms and supporting data, wetland delineation forms, any wetland assessments, and any

wildlife habitat evaluations. Classifying wetland types according to Cowardin et al. (1979) will help facilitate the Division's review. Alternative analysis reports, as required under the Rivers Protection Act, must be provided.

- Clearly delineate boundaries of proposed work on a U.S.G.S. topographic map. Avoid drawing broad circles or using arrows to indicate the project locus.

- Provide plans that show the entire proposed project on one page, including streets and other landmarks. Plans drawn at a scale of 1:40 are often easiest to interpret. Delineate the limit of clearing on plans and show grading, limit of lawn, and all other project components.

- Delineate wetland Resource Areas, including Riverfront Areas, on plans. Make sure Bordering Vegetated Wetland flag numbers are clearly visible on plans. Delineate wet depressions that may be state or federal wetlands on plans.

- Provide ground-level photographs that characterize wetland types within and near the impact area(s). Label photographs and cross-reference them on 1:40 scale plans. Providing a 1:12,000 scale, color-infrared, aerial photograph (taken when leaves are off trees) with the subject property clearly marked is recommended.

- Provide land-use information for the site and neighboring lands. Include residential and commercial development, roads, agricultural land, and active or abandoned gravel pits. Demarcate these areas on the plans, if possible.

- Include detailed erosion and sedimentation control plans, particularly for sites with steep topography and for projects that will disturb large amounts of upland adjacent to wetlands.

- Submit to the Division any new or revised information presented to the Conservation Commission during the hearing process.

Massachusetts Endangered Species Act – The Massachusetts Endangered Species Act (MESA) (MGL c. 131A) prohibits the "taking" of any species of animal or plant listed as Endangered, Threatened, or Species of Special Concern. For animals, "taking" is defined as: "to harass, harm, pursue, hunt, shoot, hound, kill, trap, capture, collect, process, disrupt the nesting, breeding, feeding, or migratory activity or attempt to engage in any such conduct, or to assist in any such conduct" (321 CMR s. 10.02). This broad definition of "take" allows regulatory protection to be provided to individual spotted turtles as well as to their wetland and upland habitats.

Under certain circumstances, the Division may grant a permit allowing the "take" of state-listed species as a result of a development project. Such "Conservation Permits" (321 CMR 10.04(3)) are granted only when there are no reasonable alternatives to the proposed project, when the project has been modified to minimize impacts to rare species and their habitats,

and when the project has been designed in such a way as to provide a "net benefit" to the population(s) of affected species. "Take" can also be allowed for research or educational purposes.

Assessing Impacts Under MESA – The Division may request additional site-specific information to aid in its regulatory review of proposed projects. This will be especially true for requests for Conservation Permits that allow limited take of spotted turtles under MESA. Although 1 to 2 years of additional data collection is unlikely to describe all habitats used by a local population of spotted turtles, it is likely to contribute information useful to the Division's review process.

In reviewing a project, the Division may request additional information on some or all of the following:

- Relative abundance of spotted turtles – This information is obtained by capturing turtles with dip nets, with traps, and by hand. Captured turtles should be individually marked, and the catch per unit effort should be calculated.

- Turtle movements and location of overwintering sites – Radio-track at least 10 adult males and 10 adult females. Track turtles for at least 2 activity seasons: from initial capture to November 15 and from March 15 to November 15 of the second season. Record locations every other day from April 15 to September 15, when turtles are most active on land. Record locations once a week during the rest of the season.

- Home range sizes and lengths – Map each turtle's movements (all radio-tracking locations) on separate 1:12,000 minimum scale air photos (leaves off, color infrared). Calculate the area (in hectares, using minimum convex polygons) and length (maximum distance between 2 outermost locations, in meters) for each turtle.

- Age classes of captured turtles – Turtle age classes are best estimated from shell morphometrics. The age structure is best interpreted from size structure of the population. Measure the following on all turtles when captured and recaptured (in millimeters): carapace length, plastron length, plastron width. Count the number of growth rings on the plastron. The number and percent of turtles with <8 growth rings on the shell, and the number and percent with plastron lengths of <75 mm should be calculated.

The Division issues permits for handling and capturing state-listed species in the field and therefore must be contacted before such activities are attempted.

GUIDELINES TO AVOID ADVERSE IMPACTS

Activities that may have adverse effects on spotted turtle habitat and/or may kill or injure adults, juveniles, hatchlings, or eggs include but are not limited to the following.

- Destroying wetland habitats by filling.

- Degrading wetland habitats by increasing erosion and sedimentation, or discharging runoff and contaminants into wetlands, or eliminating amphibians that serve as prey.

- Altering the hydrology of wetland habitats. Adding impermeable surfaces nearby, such as pavement and buildings, can alter the hydrology of wetlands by increasing runoff. Water detention systems can alter hydrology by decreasing the amount of water that normally reaches the wetland.

- Undertaking activities that cause or significantly increase the likelihood of direct mortality to turtles or eggs. Examples include: building roads and parking lots; increasing traffic on existing roads; using machinery for landscaping, forest-cutting, lawn-mowing, and plowing. The probability that mortality will occur will likely increase with increased proximity of these activities to known turtle habitat.

- Construction of barriers to turtle movements, including walls and fences, ditches, curbs, railroads (non-elevated, without underpasses or overpasses), and roads (non-elevated, without underpasses or overpasses). Barriers between overwintering wetlands and seasonal activity pools may be especially detrimental.

- Decreasing habitat diversity within wetlands or decreasing diversity and abundance of wetlands at a landscape level. Disrupting ecological processes that maintain diversity within and between wetlands may adversely impact spotted turtles. Altering hydrology by adding impervious surfaces (driveways, houses) or by installing retention basins can disrupt these processes.

- Increasing the amount of human activity in spotted turtle habitat, without providing sufficient undisturbed habitat, and without enforcing bans on the collection of spotted turtles.

Because spotted turtles commonly travel each year between habitat features that are hundreds of meters apart (Tables 2 and 3), the activities listed above have the potential to adversely affect habitat or cause "take" of spotted turtles if they occur up to 1 km from documented turtle sightings. However, not all development activities within the range of maximum movement are likely to adversely affect actual habitat areas or to cause a taking. Each proposed project will be reviewed separately by the Division, and consideration will be given to site-specific conditions, the nature and extent of the proposed activity, the extent and quality of local turtle habitat, and knowledge of both the general ecology and local status of spotted turtles.

LITERATURE CITED

Barlow, C. and B. Kingsbury. 1999. Habitat use, home range, and movement patterns of the spotted turtle in northeast Indiana. Abstracts of the joint meeting of the American Society of Ichthyologists and Herpetologists, American Elasmobranch Society, Herpetologists' League, Society for the Study of Amphibians and Reptiles, State College Pennsylvania.

Brooks, R.J., G.P. Brown and D.A. Galbraith. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69:1314-1320.

Congdon, J.D., A.E. Dunham and R.C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7(4)826-833.

Congdon, J.D., A.E. Dunham and R.C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoology 34:397-408.

Cowardin, L. V. Carter, F. Golet, and E. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service. FWS/OBS-79/31. 103 pp.

Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68(5):1412-1423.

deMaynadier, P.G. and M.L. Hunter. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management 63(2):441-450.

Doroff, A.M. and L.B. Keith. 1990. Demography and ecology of an ornate box turtle (*Terrapene ornata*) population in south-central Wisconsin. Copeia 1996(2):387-399.

Ernst, C. 1970. Reproduction in *Clemmys guttata*. Herpetologica 26:228-232.

Ernst, C. 1976. Ecology of the spotted turtle, *Clemmys guttata* (Reptilia, Testudines, Testudinidae), in southeastern Pennsylvania. Journal of Herpetology 10:25-33.

Ernst, C. and G. Zug. 1994. Observations on the reproductive biology of the spotted turtle, *Clemmys guttata*, in southeastern Pennsylvania. Journal of Herpetology 28:99-102.

Gibbs, J.P. and J.D. Amato. 2000. Genetics and demography in turtle conservation. Pp. 207-217 in M.W. Klemens (ed.), *Turtle Conservation*. Smithsonian Institution Press, Washington, D.C.

Haxton, T. and M. Berrill. 1999. Habitat selectivity of *Clemmys guttata* in central Ontario. Canadian Journal of Zoology 77:593-599.

Joyal, L. 1996. Ecology of Blanding's (*Emydoidea blandingii*) and spotted (*Clemmys guttata*) turtles in southern Maine: population structure, habitat use, movements, and reproductive biology. M.Sc. thesis, University of Maine, Orono.

Lewis, T.L. and C.A. Faulhaber. 1999. Home ranges of spotted turtles (*Clemmys guttata*) in southwestern Ohio. Chelonian Conservation and Biology 3:430-434.

Litzgus, J. and R. Brooks. 1998. Reproduction in a northern population of *Clemmys guttata*. Journal of Herpetology 32:252-259.

Milam, J. 1997. Home range, habitat use, and conservation of spotted turtles (*Clemmys guttata*) in central Massachusetts. M.Sc. thesis, University of Massachusetts, Amherst.

Perillo, K. 1998. Daily and seasonal movements of spotted turtles (*Clemmys guttata*) in relation to habitat use in north central Connecticut. M.Sc. thesis, University of New Haven, West Haven, Conn.

Raymond, L.R. and L.M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander, *Ambystoma talpoideum*, in an adjacent unaltered forest. Journal of Herpetology 25:509-512.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:491-494.